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Does endophyte influence resource acquisition and allocation in defoliated tall fescue as a function of microsite conditions?

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Abstract

Tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh.] often benefits in terms of productivity and persistence when infected with *Neotyphodium coenophialum* ([Morgan-Jones and Gams], Glenn, Bacon, and Hanlin) endophyte, but the influence of novel non-ergogenic endophytes is unclear. We conducted a field experiment using container-grown tall fescue plants to determine how plants allocated resources when clipped repeatedly in microsites differing in the amount of available light associated with open (full sun), and partially shaded (about 20 or 40% of full sun) conditions. Plants of the same tall fescue cultivar (Jesup) were host to either a native or novel non-ergogenic fungal endophyte (MaxQ^{TM}), or were devoid of endophyte. Seedlings of plants infected with the novel endophyte had slower germination, germinated later, and allocated more photosynthate to shoots than roots, when compared to J− or J+ plants. Herbage production of undisturbed canopies was not influenced by host–endophyte association within a microsite, with more herbage produced at the open than at the heavily shaded site. Clipping plants to a 5- or a 10-cm residue height tended to accentuate differences, with diminished productivity and greater variability occurring when plants were maintained at 5 cm. This trend was supported by allometric resource allocation patterns, and in terms of vegetative propagule mass relative to the number of propagules. Tall fescue, irrespective of host–endophyte association, grown as forage in silvopastoral situations should be managed to maintain no less than a 10-cm residual plant height. Trends in photosynthate allocation and plant size might influence persistence and should be investigated for more than two growing seasons.
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Keywords: Dry matter production; *Festuca arundinacea*; Growth allometry; *Neotyphodium coenophialum*; Shade; Tiller production

1. Introduction

Endophyte race (Brem and Leuchtmann, 2003) and plant host genotype (Cheplick and Cho, 2003) interact to create a continuum of morphological and biochemical responses expressed by the host–endophyte association. As an example, endophyte (*Neotyphodium coenophialum* [Morgan-Jones and Gams], Glenn, Bacon, and Hanlin) infected tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh.] used in agricultural applications often has greater yield and persistence compared to non-infected conspecifics (Bouton et al., 2001; Clay, 1998), especially where stressful growing conditions occur (Bouton et al., 1993; West et al., 1993; Malinowski et al., 2005). When consumed, endophyte-infected tall fescue can be deleterious to livestock and other herbivorous organisms because of bioprotective alkaloids produced by the association. Host–endophyte associations can be modified to produce negligible amounts of alkaloid, thus having clear and immediate benefit to grazing livestock (Parish et al., 2003). The influences of non-ergogenic endophytes on host productivity and survival in the field were reported (Bouton et al., 2002), but mechanisms of growth and persistence of non-ergogenic host–endophyte associations remain to be explained.

Allocation of dry matter (DM) among plant tissues seemed to benefit from endophyte infection (Belesky and Fedders, 1995), and allocation was influenced by host genotype and endophyte interactions (Belesky and Fedders, 1996). In some instances, however, plants without endophyte produced more tillers than did the infected isolines (Belesky and Fedders, 1996). The positive responses associated with endophyte depended on management, with minimal influence attributable to endophyte when plants were not cut. Endophyte influences on plant responses could be accentuated when plants are defoliated. Canopy management and the availability and quality of light could be

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complicated by microsite conditions associated with topography, or cultural practices such as silvopasture.

Grasses, including tall fescue, adapt to light quantity and quality (e.g., red/far-red, UV-A, and UV-B) with changes in morphology, physiology, micro-anatomy, and decreased rates of tiller production, the combined effect of which could compromise sward persistence and herbage composition (Skinner and Nelson, 1994; Monaco and Briske, 2000; Wherley et al., 2005). Stembase mass declined and photosynthate allocation changed in tall fescue growing in partial shade (Wherley et al., 2005). A similar change in photosynthate allocation and tiller production occurred in orchardgrass (*Dactylis glomerata* L.) grown and defoliated repeatedly under natural shade compared to full sun conditions (Belesky, 2005b). Could light environment interact with host–endophyte associations to influence mass allocation, tiller production, and secondary metabolites, and could management influence the response?

Once established, the productivity of tall fescue is determined by expression of new tillers, and the appearance and elongation of leaves (Nelson and MacAdam, 1989). Defoliation (clipping or grazing) disrupts the light acquisition process, so forage productivity and persistence under low irradiance depend on rapid reestablishment of post-defoliation leaf area and continued expression of new tillers to capture light and occupy sites in the sward. Understanding photosynthate allocation within the plant could help identify practices that optimize leaf production and resource use, and create desirable herbage composition. This is especially important where the co-occurring stresses of competition for light and defoliation interact to influence productivity and nutritive value (Belesky et al., 2006).

Our objective was to determine if host–endophyte association influenced productivity and DM allocation in tall fescue with a native or novel endophyte subjected to the concurrent stresses of defoliation, and restricted light associated with silvopastoral conditions. Light quantity was used as an index of site conditions, bearing in mind that changes in light quantity and spectral composition, were associated with differences in canopy and soil temperature, wind speed, and water use by the sward (Morecroft et al., 1998; Belesky, 2005a).

2. Materials and methods

2.1. Plant culture

Commercially available seed of Jesup infected with a wild-type endophyte (J+), Jesup devoid of endophyte (J−), and Jesup/MaxQ™[1] containing the novel endophyte AR542 hence referred to as MaxQ, was sown (26 seeds pot^{-1}) in 2.5 L plastic pots containing a mixture of 2 parts soil (Gilpin, fine-loamy, mixed mesic, Typic Hapludult) and 1 part sand. Soil was limed to achieve a pH of 7.0. Container-grown plants were used to minimize site and soil related effects on germination and nutrient availability (Monaco and Briske, 2000). Plants were grown for six weeks in a controlled environment room, with a 14 h photoperiod, 24/18 °C light/dark temperature and 55% relative humidity. Plants were watered as needed.

Plants were maintained out-of-doors in a non-shaded area for 18 d prior to placement at microsites in early May. The bottoms of each pot were removed at planting, pots placed firmly in the ground to ensure contact with soil, and positioned so that the soil level in pots corresponded to the surrounding soil levels. Microsites (81°7′W; 37°45′N; 850 m above sea level) included an open (OP) unobstructed site, and two edge zones representing a north edge (NE) and south edge (SE) of an opening parallel to the sun path. The NE and SE sites were about 30 m apart and the OP site midway between. Microclimate conditions for the growth interval were characterized using automated weather stations installed at each site. Atmospheric data presented in Table 1 illustrate site conditions collected at 2 m above the soil surface and include light measured with radiometric quantum (LI-190SZ, LiCor, Lincoln, Nebraska, USA) and pyranometric (CM3 Pyranometer Kipp & Zonen B.V., Delft, The Netherlands) sensors, maximum and minimum air temperature, precipitation, wind speed and relative humidity. Soil temperature was determined at the soil surface and the 5-cm depth. Values for ET_O (mm) were calculated according to the Penman–Monteith equation (Monteith and Unsworth, 1990) based on air temperature, solar radiation, wind speed, relative humidity, global position and elevation above sea level.

All plants received a split application of $Ca(NO_3)_2$ and KH_2PO_4 to supply a total of 120, 160, and 200 kg ha^{-1} N, P, and K, with half of the season total applied when plants were placed at each microsite and half at mid-season. Plants were watered (500 mL pot^{-1}) whenever precipitation was minimal during the growing season.

A mixture of orchardgrass, perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) was sown to create forage sward buffers with canopy characteristics similar to the experimental plants at each microsite. The forage buffers were clipped to either 5- or 10-cm height each time experimental tall fescue plants were clipped. Fertilizer was applied in the same manner as supplied to the experimental plants.

2.2. Sample collection and analysis

Baseline data were collected from 18 replicates (9, 5-cm residual plant height and 9, 10-cm residual plant height), immediately prior to planting time, at which time all plants were clipped to their respective 5- or 10-cm residual plant height. Three replicates of each of the three tall fescue associations were collected and a destructive sampling made each time mean plant height reached 20 cm. Total tiller number, tillers in the harvest zone, and mass of leaf (>5 or 10 cm above soil surface), stembase (soil surface to 5 or 10 cm), and root was determined. Remaining experimental plants were clipped to their respective residual plant height and allowed to re-grow to 20 cm. Three replicates of each association were maintained as undisturbed canopies at each microsite until the end of the growing season. The undisturbed plants were removed in late autumn and

[1] Trade names are used for the convenience of the reader and do not imply endorsement by USDA over comparable products and services.

Table 1
Total monthly precipitation, mean temperature, and total photosynthetically active photon flux density (PPFD) of the 2004 growing season

	Open (OP)	North edge (NE)	South edge (SE)
PPFD ($mol\,m^{-2}$)[a]	5262	1983	1004
ET_O[b]			
April	105.16	84.44	58.35
May	139.27	65.95	36.08
June	130.47	38.81	23.76
July	135.84	43.42	23.30
August	132.97	53.11	18.97
September	99.57	60.77	14.46
October	55.75	51.08	13.87
Precipitation (cm)			
April	13.00	11.38	12.04
May	19.18	15.44	12.45
June	17.04	11.38	–[c]
July	14.58	9.78	–
August	5.49	3.73	5.46
September	14.99	10.00	12.04
October	8.61	6.05	6.86
Min temp (°C)			
April	5.24	5.28	5.68
May	12.56	12.68	13.12
June	13.85	13.95	14.40
July	16.23	16.32	16.78
August	13.97	14.14	14.57
September	12.97	13.11	13.45
October	8.05	8.17	8.55
Max temp (°C)			
April	17.90	17.74	17.99
May	25.44	24.63	24.47
June	25.22	23.84	23.65
July	26.57	25.58	25.00
August	25.68	24.99	24.10
September	24.30	24.08	22.22
October	19.17	19.90	18.04

Data are for open (OP), north edge (NE) and south edge (SE) of sun path forest clearing at 81°7′W; 37°45′N; 850 m above sea level in the central Appalachian Region of the eastern USA.
[a] Light data (PPFD) collected 1 April through October 31.
[b] Potential evapotranspiration computed according to Monteith and Unsworth (1990).
[c] Equipment failure. No data for these months.

partitioned into leaf, stem, root, and senesced tissue. All tissues were lyophilized, ground, and dry mass determined.

2.3. Parameter calculations

All calculations are on a per tiller basis, with leaf data normalized for either 10 or 15 cm of top growth. A linear, allometric regression equation was used to model DM allocation as a function of plant size (Shipley and Meziane, 2002). The calculation used in this experiment included stembase as part of the leaf and assumed the form:

$$\ln(M_s) = a + b\,\ln(M_r) \tag{1}$$

where M_s = DM (g) of shoot (leaf + stembase) and M_r = DM (g) of root.

Stembase was included in the shoot component because this is the source of new leaves, and nonstructural carbohydrates accumulate there in cool-temperate perennial grasses.

Instantaneous growth rates were derived from the Gompertz growth model (Draper and Smith, 1981), of cumulative yield data as influenced by fescue association, microsite, and residual plant height.

$$\omega = \alpha\, e^{-\beta \exp(-kt)} \tag{2}$$

where ω = cumulative mass (mg tiller^{-1}), t = day, e ≈ 2.718, and the calculated regression parameters α (asymptotic yield), β (time function) and k (dimensionless).

Calculated regression parameters were derived from the PROC-NLIN procedure of SAS.

2.4. Statistical analysis

Dry matter (total, leaf, stembase, root) number of tillers, and shoot:root ratios were analyzed as repeated measures with SAS-MIXED procedures (Littell et al., 1996). Replication and interactions with replication were random. Fescue association, residual plant height, and harvest were modeled as fixed effects in each site and were analyzed as a repeated measures analysis with SAS-MIXED procedures using SUBJECT and GROUP options. The SUBJECT option for microsite specifies that the intercept and slope effect of one microsite is independent of the intercept and slope of other microsites, but correlated within each microsite. The GROUP option for fescue association addresses the different covariance parameters associated with each association harvested at varying time intervals in the growing season. Undisturbed canopies were analyzed separately. Denominator degrees of freedom were calculated using the Satterthwaite option. Cumulative leaf, shoot (leaf + stembase), and root yield data were analyzed using SAS-MIXED procedure and regression analysis to determine goodness-of-fit based on host endophyte association, residue height and seasonal distribution. Associations were separated in the model for analysis of site and residual plant height.

3. Results and discussion

3.1. Germination and seedling growth

We observed earlier that host–endophyte association influenced establishment (germination) and consolidation (tillering), but not growth mechanisms such as leaf appearance and elongation of 42-d-old Jesup seedlings (Belesky and Burner, 2004). Findings corresponded with reports that endophyte influenced seedling germination in certain grasses (Clay, 1987; Bacon, 1993). A comprehensive assessment of host–endophyte associations showed that germination percentages were greater in endophyte-free than infected tall fescue seed (Owens et al., 2007). Interestingly, seedling mass was less for endophyte-free compared to infected plants, and tiller production varied widely. They concluded that novel endophytes contributed to superior germination and seedling vigor when

Table 2
(a) Total leaf production ((live and dead) per tiller), and (b) seasonal growth interval and number of harvests per season for host–endophyte associates (FA) J+, J− and MaxQ as a function of microsites open (OP), north edge (NE) and south edge (SE) edge of a sunpath forest clearing and residual sward height (5 or 10 cm) at 81°7′W; 37°45′N; 850 m above sea level in the central Appalachian Region of the eastern USA

FA	Serial cuts						Undisturbed		
	OP		NE		SE		OP	NE	SE
	5 cm	10 cm	5 cm	10 cm	5 cm	10 cm			
(a) Total leaves tiller^{-1}/Total dead leaves tiller^{-1}									
J+	7/4	6/4	7/5	5/3	5/3	5/3	6/2	5/2	6/3
J−	7/5	7/5	5/3	5/3	4/2	5/3	6/2	5/3	5/2
MaxQ	5/3	6/4	6/4	6/4	4/2	4/3	6/2	5/2	5/3
(b) Growth interval (d)/Number of harvests									
J+	131/4	123/6	88/3	89/6	88/4	87/6	153	153	153
J−	131/4	144/6	108/3	89/6	66/3	87/6	153	153	153
MaxQ	131/4	131/6	116/3	105/6	88/4	87/6	153	153	153

compared to a similar genotype infected with native endophyte.

In our previously reported experiments, germination (percentage) of MaxQ was less, and maximum rate of germination occurred several days later when compared to J+ or J− plants grown in a controlled environment. Whole plant DM and the allocation of photosynthate among plant parts of seedlings were influenced by host–endophyte association, with MaxQ plants being relatively smaller, but allocating a greater proportion of photosynthate to shoots than roots (Belesky et al., 2004). The greater allocation to shoots could facilitate competitiveness with other plants in the above-ground portion of a sward, but jeopardize persistence if the allocation pattern persisted throughout the life of the plant. Gundel et al. (2006) make an interesting point suggesting that endophyte in *Lolium multiflorum* seeds may be associated with environment sensing (e.g., light quality) rather than having a direct influence on germination rate.

Trends occurring at the seedling stage could have long-term influence on competitive fitness that could eventually influence sward composition as a function of endophyte infection status, such as the decreased persistence of grazed stands of J− and MaxQ observed by Bouton et al. (2002). Could the differences observed at the seedling stage of J+, J−, and MaxQ influence persistence and productivity of plants subjected to concurrent stresses associated with defoliation and varying degrees of resource availability; in this case light?

3.2. Undisturbed canopies

Many ecophysiological experiments designed to characterize resource allocation involve undisturbed canopies representing standing crop productivity. When Jesup-endophyte associations, i.e., J+, J−, and MaxQ, grew undisturbed for 153 d in the field each tiller produced the same number of leaves (Table 2a); however, whole plant mass differed as a function of microsite (Fig. 1). Total DM was greatest at the OP site and least at SE, irrespective of host–endophyte association (Fig. 1). In previous experiments, endophyte infection had minimal influence on total DM or allocation to above and belowground structures of uncut tall fescue–endophyte associations (Belesky and Fedders (1995); but did influence total stembase mass and mass per tiller (Belesky and Fedders, 1996). Stembases of cool-temperate grasses are important components contributing to stress survival and post-defoliation regrowth mechanisms. Nonstructural carbohydrate accumulation and tiller bud initials occur in the pseudostem, facilitating post-defoliation regrowth and competitive ability. One approach to sustaining stembase mass would be to manage defoliation events to create conditions that stimulate tiller initiation. Relatively long intervals between defoliation events could sustain stembase mass but might cause self-shading, leading to fewer tillers and less shoot mass (Kays and Harper, 1974), leaf senescence exceeding leaf appearance (Parsons et al., 1988), and an overall decline in sward productivity and persistence. Differences observed at the seedling stage could be amplified once defoliation is imposed.

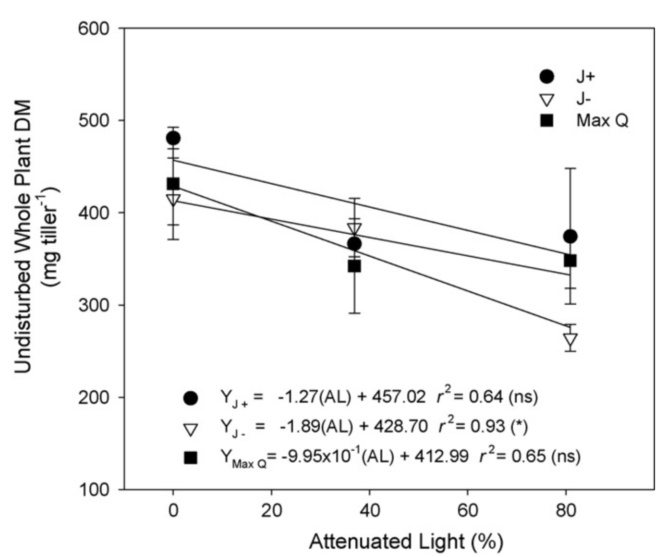

Fig. 1. Whole plant dry matter and regression equations for undisturbed canopy of host–endophyte associations J+, J− and MaxQ as a function of microsite with 0, 35.9 and 80.9% attenuated light (AL). ns, not significant; $^{*}P < 0.05$.

3.3. Defoliated canopies

In the controlled environment experiments that preceded the field experiment reported here, the rate of tiller production or leaf DM did not differ between MaxQ and the naturalized association of J+ tall fescue (Belesky et al., 2004). However, whole plant DM and allocation of photosynthate between root and shoot was influenced by host–endophyte association, with MaxQ plants being relatively smaller and allocating more photosynthate to shoots than roots. Growth rates and the time at which maximum growth was achieved were comparable among host–endophyte associations clipped at 1- or 2-wk frequencies. When clipped at 3-wk intervals MaxQ had 10% lower rate of growth and reached maximum productivity 14 d later than J+. Although smaller in total mass and having fewer tillers, MaxQ plants displayed more leaf and had larger stembases than J+ or J−, and would be likely to be very competitive with other plants in the above-ground portion of a sward. Low tiller production could influence long-term persistence and warranted investigation under field conditions.

The duration of sustained growth in field-grown Jesup tall fescue varied with site and the residue height to which plants were clipped (Table 2b). Four clips were made when plants were maintained at a 5-cm residue at the OP and SE sites and three when plants were growing at the NE site. Six clips were made at each of the sites when plants were cut to a 10-cm residue.

The interaction of microsite, host–endophyte association, harvest date, and residue height influenced DM for each structural component. In particular, total leaf DM of MaxQ and J− was greater when plants were clipped to a 10-cm rather than 5-cm residue at each microsite, whereas J+ leaf DM was greater when clipped to a 10-cm residue at the NE site and was not significantly different from the 5-cm residue when growing at the OP or SE sites (Table 3). Typically, clipping to remove a greater portion of the canopy leads to greater DM yields (Burns et al., 2002); however, the response is mediated in part by canopy height at the time of defoliation. We imposed clipping when mean canopy height reached 20 cm, regardless of frequency or duration of regrowth intervals. The 10-cm residue management was derived from earlier results that led to sustained productivity for orchardgrass grown under a range of tree-induced shade conditions (Belesky, 2005a,b), and for repeatedly defoliated tall fescue (Belesky and Fedders, 1996). The OP and SE sites represent extremes in light availability with the possibility of too little light at SE (about 20% of the season total PPFD), especially after mid-day, or essentially unlimited light at OP with the co-occurring stresses of high leaf temperature and high evaporative demand relative to the other microsites (Table 1). As such, management practices should be designed to obtain the desired plant response with respect to the interaction of plant growth strategies with microsite conditions.

Greater variation in whole plant DM was associated with the 5-cm compared to the 10-cm residue height. For example, the 10-cm rather than 5-cm residue led to at least a 4-fold increase in stembase mass, irrespective of association (Table 3).

Table 3
Cumulative yield of leaf, stembase and root dry matter (DM) for host endophyte associations (FA) J+, J− and MaxQ clipped to a 5- or 10-cm residue (R) as a function of microsite (S) including, open (OP), north edge (NE), and south edge (SE) of a sun-path forest clearing at 81°7′W; 37°45′N; 850 m above sea level in the central Appalachian Region of the eastern USA

FA	OP		NE		SE	
	5 cm	10 cm	5 cm	10 cm	5 cm	10 cm
Leaf DM (mg tiller^{-1})						
J+	88.1 ± 3.5	85.3 ± 1.6	40.1 ± 2.0	51.4 ± 1.4	48.3 ± 2.0	51.1 ± 1.2
J−	77.6 ± 2.7	82.1 ± 1.5	43.0 ± 2.8	54.6 ± 1.2	35.5 ± 2.0	46.0 ± .76
MaxQ	80.6 ± 2.7	90.7 ± 1.5	43.7 ± 3.5	52.3 ± 1.0	40.9 ± .94	46.5 ± .62
Stembase DM (mg tiller^{-1})						
J+	8.4 ± 0.21	34.4 ± 0.94	3.9 ± 0.03	28.6 ± 0.32	5.0 ± 0.14	25.2 ± 0.36
J−	6.9 ± 0.08	32.1 ± 0.56	3.7 ± 1.20	25.9 ± 0.31	3.9 ± 0.17	20.9 ± 0.26
MaxQ	9.0 ± 0.22	33.5 ± 0.51	4.6 ± 0.29	25.3 ± 0.23	5.3 ± 0.09	22.8 ± 0.18
Root DM (mg tiller^{-1})						
J+	40.4 ± 3.1	62.3 ± 1.84	21.0 ± 3.9	34.9 ± 0.43	18.5 ± 0.48	27.9 ± 0.44
J−	28.2 ± 1.0	70.0 ± 2.8	17.2 ± 3.1	31.9 ± 0.43	12.3 ± 0.68	22.9 ± 0.49
MaxQ	41.9 ± 3.0	71.8 ± 2.2	19.7 ± 2.9	34.9 ± 0.81	15.2 ± 0.86	26.4 ± 0.52

Analysis of variance for component cumulative yield

	Leaf			Shoot			Root		
	J+	J−	MaxQ	J+	J−	J+	J+	J−	MaxQ
S	57.17***	63.38***	63.83***	11.21**	8.17**	7.83**	15.94***	57.53***	32.61***
R	1.21 ns	8.73*	5.90*	419.64***	216.84***	166.24***	12.05**	79.12**	23.29***
$S \times R$	1.41 ns	0.53 ns	0.16 ns	2.32 ns	2.69 ns	1.59 ns	0.70 ns	15.04***	2.15 ns

Values are means and ±standard error of the means (ns, not significant).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Table 4
Regression parameters (α,β, k), inflection points (IP) and coefficient of determination (R^2) of nonlinear regression models for the influence of defoliation residue height (5 or 10 cm) on production of dry matter per tiller of host–endophyte associations (Jesup infected, J+; Jesup endophyte-free, J−; and MaxQ) as a function of microsite including open (OP), north edge (NE), and south edge (SE) of a sun-path forest clearing at 81°7′W; 37°45′N; 850 m above sea level in the central Appalachian Region of the eastern USA

Site	Association	Residue height (cm)	α	β	k	IP	R^2
OP	J+	5	179.600	7.619	0.0096	211	0.999
	J+	10	110.000	26.400	0.0107	307	0.995
	J−	5	115.100	10.565	0.0134	176	0.999
	J−	10	93.922	31.653	0.0204	170	0.998
	MaxQ	5	98.799	14.971	0.0166	163	0.999
	MaxQ	10	112.600	24.153	0.0182	175	0.998
NE	J+	5	49.953	27.733	0.0224	150	0.999
	J+	10	67.177	28.313	0.0213	157	0.997
	J−	5	48.390	24.026	0.0225	142	0.999
	J−	10	66.876	41.437	0.0241	155	0.995
	MaxQ	5	45.553	55.698	0.0295	137	0.999
	MaxQ	10	59.554	49.544	0.0251	153	0.994
SE	J+	5	62.994	24.803	0.0209	154	0.999
	J+	10	65.047	38.598	0.0235	156	0.998
	J−	5	50.777	29.358	0.0227	150	0.999
	J−	10	60.945	35.625	0.0224	160	0.991
	MaxQ	5	55.087	32.624	0.0217	161	0.998
	MaxQ	10	61.543	39.854	0.0230	160	0.994

See Fig. 2.

Maintaining a 10-cm residue could help reduce variation in productivity by providing a buffer of nonstructural carbohydrates in the stembase that facilitates leaf regrowth and expression of new tillers. This response could contribute to increased herbage availability for grazing livestock, and improved stand persistence (Fulkerson and Donaghy, 2001).

Maximum instantaneous growth rates (Table 4) for J+ plants at OP were less when plants were clipped to a 5 rather than

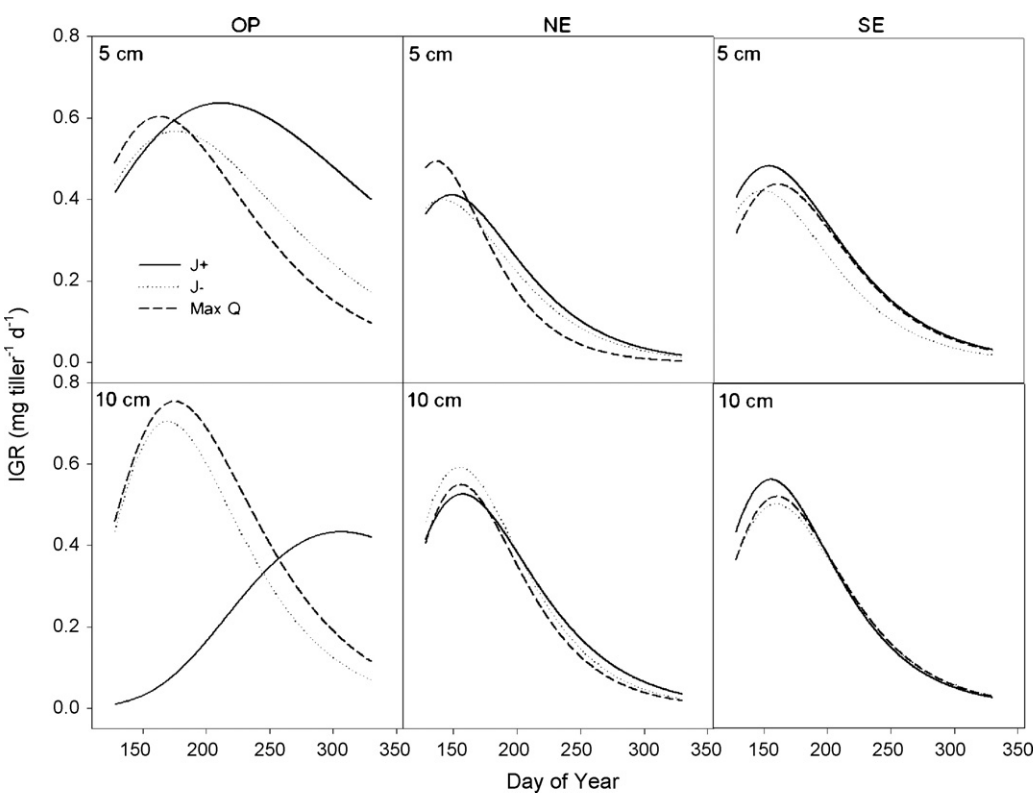

Fig. 2. Instantaneous growth rates (mg tiller^{-1} d^{-1}) derived from the Gompertz growth model of cumulative yield for host–endophyte associations J+, J− and MaxQ clipped to a 5- or a 10-cm residue and grown at open (OP), north edge (NE) and south edge (SE) microsites. Inflection points and nonlinear regression parameters are presented in Table 4.

a 10-cm residue, whereas the opposite occurred for J− and MaxQ plants (Fig. 2). Maximum growth rates for plants grown in partially shaded sites occurred early in the growing season, regardless of residue height or association. Variation among growth rates was less for plants growing at the NE and SE sites, irrespective of host–endophyte association. Plants growing at OP were not light-limited, but those at SE were. In either situation, J+ plants seemed to be able to sustain growth (OP) or had a greater rate of growth (SE) enabling plants to maintain competitive advantage. Similar growth patterns were observed for endophyte-infected relative to non-infected tall fescue plants in other investigations of response to defoliation and abiotic

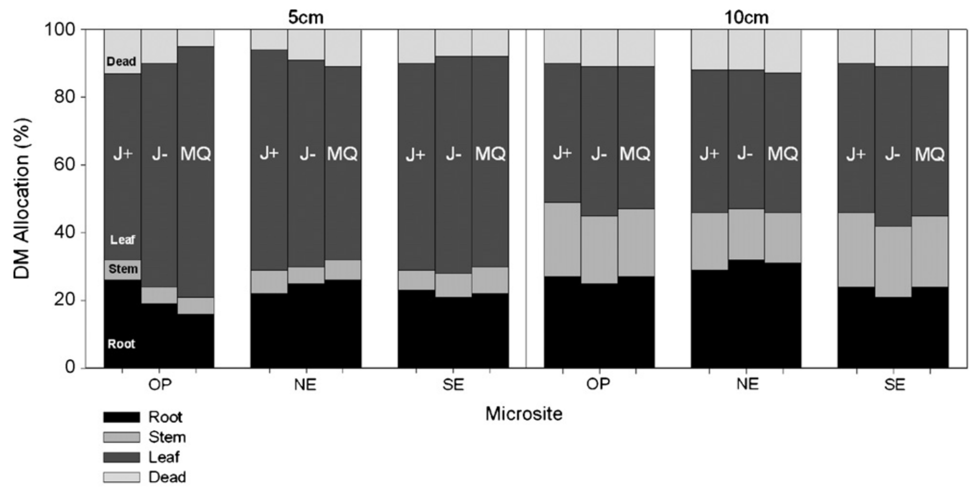

Fig. 3. Allocation of dry matter (DM) as a percentage of total plant DM, for host–endophyte associations J+, J− and MaxQ clipped to a 5- or a 10-cm residue and grown at open (OP), north edge (NE) and south edge (SE) microsites (see Table 3).

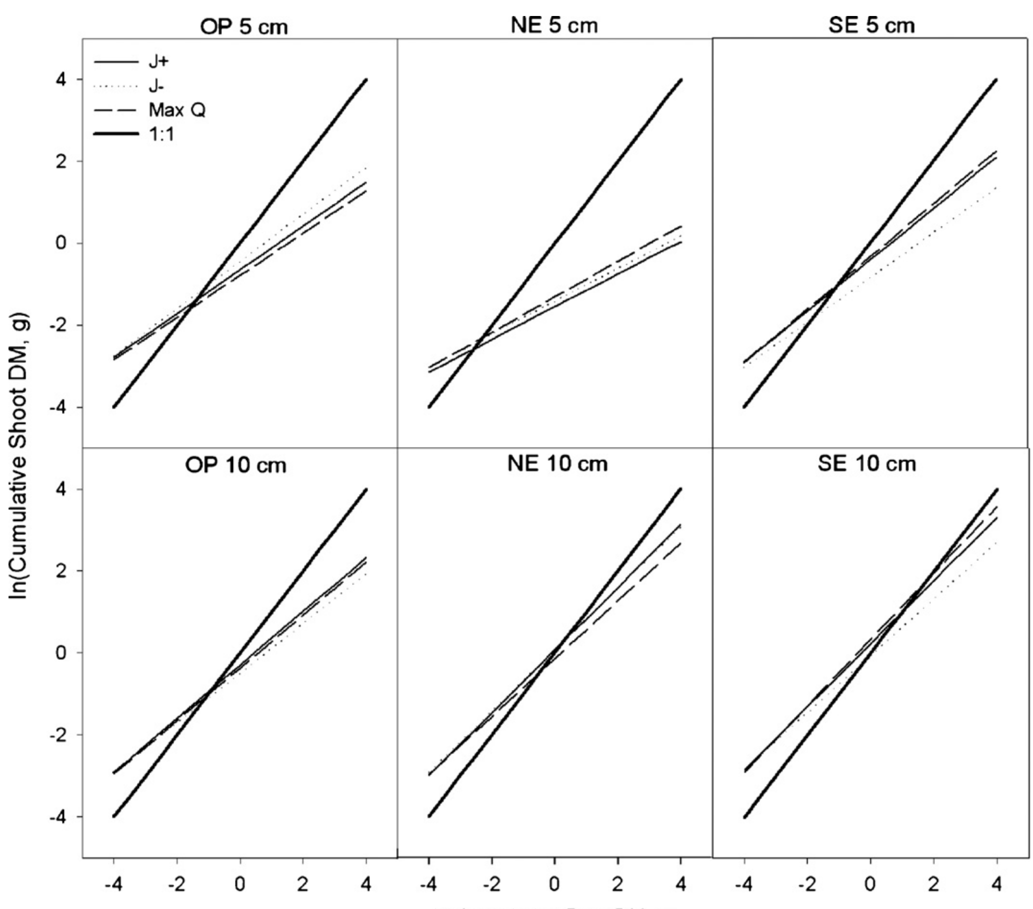

Fig. 4. Allometric relationship of shoot and root mass for host–endophyte associations J+, J− and MaxQ clipped to a 5- or a 10-cm residue and grown at open (OP), north edge (NE) and south edge (SE) microsites. Allometric regression equations are presented in Table 5.

stresses (Belesky and Fedders, 1995, 1996; Belesky and Hill, 1997). The influence of host–endophyte association on DM yield tended to be small relative to photosynthetically active radiation and irrigation for tall fescue plants clipped to 5 cm (Burner, unpublished data).

Root mass differed as a function of site, with root mass decreasing from OP > NE > SE (Table 3). The SE site tended to have the least amount of incident radiation throughout the growing season when compared to OP and NE sites. These observations correspond to literature showing that root growth of *Festuca ovina* and the consequent input of carbon to soil were controlled by radiation flux not temperature (Fitter et al., 1998). Root mass was greater for plants clipped to a 10-cm rather than a 5-cm residue, regardless of host–endophyte association.

Plants clipped to a 5-cm residue height were not as productive (in terms of leaf mass) as plants maintained at the 10-cm residue, although the 5-cm residue plants allocated a greater relative proportion of total DM to leaves than to stembase when compared to the 10-cm plants (Fig. 3). Plants maintained about the same relative allocation of DM to roots when expressed as a fraction of total DM, regardless of the residual plant height. The relative allocation patterns may not be accurate representations of how photosynthate is partitioned because plant growth patterns and associated functions differ with size (Farrar and Gunn, 1998). Allometric analysis incorporates plant size or scaling into computations of plant mass to help minimize bias when making comparative DM allocation patterns.

Relatively more DM was allocated to root than shoot of plants clipped to the 5 cm residual height (Fig. 4) when data were subjected to allometric analysis (Table 5). The plants clipped to 10 cm residue height approached a balanced (1:1) allometric S:R photosynthate allocation. Based on previous work with orchardgrass (Belesky, 2005a,b), the allometric allocation patterns of 5-cm residue plants were similar to juvenile or non-vernalized orchardgrass plants, whereas plants maintained at the 10-cm residue were similar to vernalized orchardgrass plants reflecting a stable and predictable growth model. Smaller plants tended to allocate more photosynthate to shoots than roots. As plants increased in total phytomass, allocation to shoots increased relative to allocation to roots. Trends related to host–endophyte associations were not consistent.

Table 5
Allometric regression equations computed according to Shipley and Meziane (2002) for shoot and root dry matter for open (OP), north edge (NE) of sun path and south edge (SE) of sun path at 5 and 10 cm residue height as a function of fescue association in the central Appalachian Region of the eastern USA

OP 5 cm	
J+	$\ln(M_s) = -0.65 + 0.53\ln(M_r)$, $R^2 = 0.998$, $SE_{est} = 0.04$
J−	$\ln(M_s) = -0.44 + 0.58\ln(M_r)$, $R^2 = 0.996$, $SE_{est} = 0.07$
MaxQ	$\ln(M_s) = -0.79 + 0.51\ln(M_r)$, $R^2 = 0.998$, $SE_{est} = 0.05$
OP 10 cm	
J+	$\ln(M_s) = -0.29 + 0.65\ln(M_r)$, $R^2 = 0.998$, $SE_{est} = 0.03$
J−	$\ln(M_s) = -0.50 + 0.61\ln(M_r)$, $R^2 = 0.996$, $SE_{est} = 0.01$
MaxQ	$\ln(M_s) = -0.37 + 0.64\ln(M_r)$, $R^2 = 0.998$, $SE_{est} = 0.03$
NE 5 cm	
J+	$\ln(M_s) = -1.54 + 0.40\ln(M_r)$, $R^2 = 0.967$, $SE_{est} = 0.22$
J−	$\ln(M_s) = -1.41 + 0.40\ln(M_r)$, $R^2 = 0.975$, $SE_{est} = 0.18$
MaxQ	$\ln(M_s) = -1.29 + 0.43\ln(M_r)$, $R^2 = 0.967$, $SE_{est} = 0.03$
NE 10 cm	
J+	$\ln(M_s) = 0.07 + 0.76\ln(M_r)$, $R^2 = 0.996$, $SE_{est} = 0.06$
J−	$\ln(M_s) = 0.07 + 0.75\ln(M_r)$, $R^2 = 0.994$, $SE_{est} = 0.07$
MaxQ	$\ln(M_s) = -0.15 + 0.71\ln(M_r)$, $R^2 = 0.995$, $SE_{est} = 0.06$
SE 5 cm	
J+	$\ln(M_s) = -0.41 + 0.63\ln(M_r)$, $R^2 = 0.997$, $SE_{est} = 0.07$
J−	$\ln(M_s) = -0.84 + 0.55\ln(M_r)$, $R^2 = 0.998$, $SE_{est} = 0.07$
MaxQ	$\ln(M_s) = -0.33 + 0.64\ln(M_r)$, $R^2 = 0.991$, $SE_{est} = 0.13$
SE 10 cm	
J+	$\ln(M_s) = 0.23 + 0.77\ln(M_r)$, $R^2 = 0.996$, $SE_{est} = 0.07$
J−	$\ln(M_s) = -0.06 + 0.69\ln(M_r)$, $R^2 = 0.993$, $SE_{est} = 0.08$
MaxQ	$\ln(M_s) = 0.34 + 0.81\ln(M_r)$, $R^2 = 0.992$, $SE_{est} = 0.10$

M_s = Dry mass of leaf + stembase (g), M_r = dry mass of root (g).

3.4. Tiller production

Mass per tiller expressed relative to the number of tillers produced reflected the allometric S:R patterns of DM allocation, where plants clipped to a 5-cm residue displayed substantially more variation than did plants clipped to the 10-cm residue height (Fig. 5). In general, microsite conditions influenced

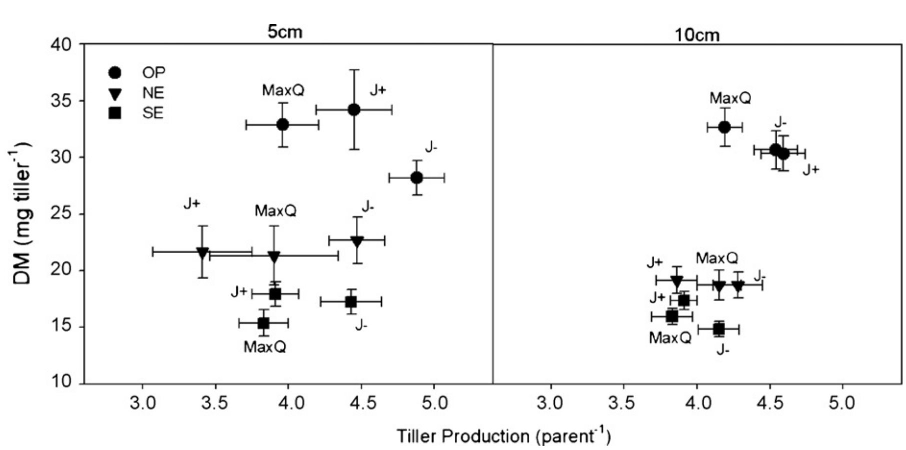

Fig. 5. Dry matter mass per tiller expressed as a function of tiller number for host–endophyte associations J+, J− and MaxQ clipped to a 5- or a 10-cm residue and grown at open (OP), north edge (NE) and south edge (SE) microsites. Bars (vertical and horizontal) represent standard error of the means.

($F = 31.93^{***}$) DM per tiller with the tendency for plants growing at OP to produce tillers that clearly were more massive than those produced at either NE or SE sites. Burner (unpublished data) obtained similar tillering results for alley-cropped tall fescue. The number of tillers produced by plants clipped to the 5-cm residue varied from 80 to 135 tillers 182 cm^{-2}, whereas the range was from 95 to 120 tillers 182 cm^{-2} when clipped to a 10 cm residue. The differences among host endophyte associations also were greater when plants were clipped to the 5-cm compared to the 10-cm residue. For example, MaxQ produced about 100 tillers 182 cm^{-2} irrespective of microsite, while mass per tiller ranged from about 15 mg for plants growing at SE to about 33 mg for plants growing at OP. Interestingly, the range in mass per tiller was similar for the 5- and 10-cm residue treatments. Maintaining the 10-cm residue seemed to minimize variation in tiller mass and tiller number when compared to the 5-cm residue. From a practical perspective, intensive canopy removal, simulated by clipping to a 5-cm residue, such as might occur in continuously grazed or dense stocking rate situations would very likely accentuate expression of certain beneficial or detrimental features of the associations on host growth.

4. Conclusions

The concurrent stresses of defoliation and resource competition (e.g., competition for light among forage plants growing in a highly productive sward, or in the shade of associated trees in silvopasture) can elicit trade-offs in terms of total productivity, allocation of photosynthate, and in turn, chemical composition. No clear influence of endophyte infection was evident when Jesup tall fescue, infected by a native or an introduced, novel endophyte was grown under a range of available light situations in the field. Seedlings of MaxQ appeared to be slightly slower in rate of germination, and allocated more photosynthate to shoots than roots, when compared to J− or J+ plants. Clipping plants to a 5- or a 10-cm residue height tended to accentuate differences, with diminished productivity and greater variability in response when plants were maintained at 5-cm. This tendency was reflected in allometric resource allocation and in the mass of vegetative propagules (tillers) relative to the number of propagules. Tall fescue grown as forage in silvopastoral situations should be managed to maintain no less than a 10-cm residual plant height. Trends in photosynthate allocation and plant size might have some influence on persistence over a longer interval of time. Shade avoidance responses could be mediated by the production of phenolic hormones (Cipollini, 2004). Endophyte-infected tall fescue produced phenolic compounds when stressed (Malinowski et al., 1998; Zhou et al., 2003), which might influence plant response to shade (Close and McArthur, 2002), impact plant persistence through resistance to herbivory and disease (Mauch-Mani and Metraux, 1998), and would probably influence herbage nutritive value.

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